



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

The complete paper describing these results and discussing them further will shortly be published elsewhere.

¹ Pearl and Surface, *J. Biol. Chem.*, **19**, 263–278 (1914); and *Ibid.*, **21**, 95–101 (1915).

² Pearl, R., *J. Biol. Chem. (in press)*, 1916).

³ Güdernatsch, J. F., *Arch. Entw.-Mech.*, **35**, 457 (1912); also *Amer. J. Anat.*, **15**, 431–478 (1914).

A PRELIMINARY REPORT ON FURTHER EXPERIMENTS IN INHERITANCE AND DETERMINATION OF SEX

By Richard Goldschmidt

(Of the Kaiser Wilhelm Institut für Biologie, Berlin)

OSBORN ZOOLOGICAL LABORATORY, YALE UNIVERSITY

Received by the Academy, November 29, 1915

In two former papers¹ the interesting ‘gynandromorphism’ produced by crossing the European and the Japanese races of the gipsy-moth (*Lymantria dispar*) was described and an experimental analysis of the phenomenon was attempted. From the data obtained important conclusions on the sex-problem in general were drawn. Although the main points seemed to be clear, a series of questions still remained open. One of them was, that the (apparently) same kind of crosses did not give the same results, if the material used had a different origin. It could be regarded as practically certain that the chief result, viz., the appearance of gynandromorphism in certain crosses found its right explanation in the hypothesis of a quantitatively different behavior or a different potency of the male sex-factors in the different races. Some of the experiments led me to suspect that this potency varied with the geographical distribution of the moth. Therefore it was one of my aims during a sojourn in Japan, to study the behavior of different local forms in that country in various crosses *inter se* and with different European forms.² These experiments are in no way to be regarded as completed, but the results so far obtained are so interesting and seem to bring the definitive solution of the problem so near, that a preliminary report on a part of them may be made.

A few words are first needed about the terminology. In previous papers I have used the term of gynandromorphism to indicate the sexual abnormalities produced in the racial crosses of these moths. It seems, however, no longer advisable to use this term, as it is applied more or less generally to quite a different phenomenon, *i.e.*, to individuals showing a mosaic of the characters of both sexes. In such a gynandromorph—see for example Boveri’s late analysis of the Eugster bees³—a given organ or complex of cells is either male or female. But this

is not the case with my moths; the entire individual represents a definite, quantitatively fixed stage intermediate between the two sexes. If we represent femaleness and maleness as the end points of a series, say one as 0 and the other as 100, a given specimen of these 'gynandromorphic' moths would be represented by the points 12 or 35, etc. These animals do not represent a mixture of the characters of the two sexes, but a definite point between the two extremes, maleness and femaleness. In the former papers some characters were thought to be a mosaic, viz., the color of the wings, which shows in certain stages definite patches of male and female design. It is now clear that this is but a consequence from the physiology of pigmentation, a fact that later will be the starting point for important theoretical discussions. So it seems advisable to introduce a new term to designate the phenomenon treated in these experiments. I shall call in the future the different sexual intermediates *intersexes*; female intersexes, if they are genetically females, but transformed to some stage towards maleness, and male intersexes if the transformation goes in the opposite direction; the whole phenomenon being called intersexualism.⁴

Before describing the new results a short account might be given of the different stages of intersexualism so far produced in the experiments. Every single step has now been bred from a normal female through the different grades of female intersexes to a normal male; also the steps starting from the normal male through male intersexes towards the female up to three-fourths of the way. Every single one of these steps can be produced now at will by crossing the right combination of races. Female intersexualism begins with animals, which show feathered antennae of medium size (feathered antennae are a male character) but which are otherwise entirely female in appearance except that they produce a smaller number of eggs, which are fertilized normally. In the next stage patches of the brown male pigment appear on the white female wings, in steadily increasing quantity. The instincts are still female, the males are attracted and copulate. But the characteristic egg sponge laid by the animal contains nothing but anal hairs, in spite of the fact that the abdomen is filled with ripe eggs. In the next stage whole sections of the wings show male coloration, with cuneiform female sectors between, the abdomen becomes smaller, contains fewer ripe eggs, the instincts are only slightly female, the males are attracted very little, and reproduction is impossible. In the next stage the male pigment covers practically the whole wing, the abdomen is almost male, but still contains ovaries with a few ripe eggs, the instincts are intermediate between males and females. Then follow very male-like animals, which still

show in different organs their female origin and have rudimentary ovaries. They lead to practically male-like animals, called 'female-males' in my former paper, containing gonads which exhibit all transitional stages from an ovary to a testis. The end of the series is formed by males, which show in some minor characters, such as the shape of wings, still some traces of their female origin.

The series of the male intersexes starts with males showing a few white female spots on their wings. These become larger and larger, the amount of brown pigment correspondingly decreasing, finally (in extreme specimens) leaving only a few granules along the veins. Hand in hand with this the abdomen increases in size, reaching in the most extreme case two-thirds of the female size (without containing eggs!). The same is true for the instincts, which become more and more female. Further, the copulatory organs, which show in the female intersexes also a complete series of gradations from femaleness to maleness, and finally in the testis, which shows the first steps of transformation into an ovary.

There is another new point to be mentioned in this connection, as the fact that it was unknown is probably responsible for some errors in my former papers. It has been noticed that there are Japanese races, which contain a wing-pigmentation factor in the female sex; and the effect produced can be increased in certain crosses. In this way females with pigmented wings may arise, which may be mistaken for intersexes, and if this phenomenon occurs together with slight intersexualism, low grade intersexes may be mistaken for high grade ones. The further investigation of this will be of importance.

Going over now to the breeding results, we shall describe first only those relating to the female intersexes. It was found that there are in the European as well as in the Japanese forms, definite races possessing a special potency of the male sex-factors. If we cross forms of like or similar potency, the offspring is normal. But if we cross races with different potency of the male factors we get in F_1 female intersexes, provided the mother belongs to the race of lower potency. The degree of intersexuality depends of course upon the difference of the potencies. The European races so far known to me all show low potency; and in the Japanese races all grades are found from the lowest to the highest potency of those factors. If now any European race is crossed in any direction with one of the 'weak' Japanese races (the races K, Fu, M, H of my records) only normal females appear in the offspring. The same naturally holds true for crosses of any of these forms *inter se*. But all European females and also the females of the weak Japanese races,

crossed with males of the 'strong' Japanese races (*i.e.*, G, O, A) ought to yield female intersexes, the grade of intersexuality depending upon both races involved in the cross. In detail the main results are the following; the F₁ males being left out of account:

1. All possible F₁ combinations between the weak Europeans S and F and the weak Japanese K, Fu, M, H contain only normal females.

2. Males of the moderately strong Japanese race G crossed with the very weak European females F produce nothing but high grade female intersexes ranging almost up to the above quoted 'female-males.' The same males produce, if crossed with the somewhat less weak European race S, nothing but medium female intersexes. The same males again crossed with the still less weak Japanese race H give in F₁ low grade female intersexes; and finally from the cross between these males and the highest of the weak Japanese races, K, we get only slight female intersexualism. There is to be added that the intersexuality affects every single individual that is genetically (one X-chromosome) a female.

3. Another of the Japanese races, which has a higher potency than G, produces in similar crosses with the weak European races the highest grade of female intersexuality, the so-called 'female-males.'

4. If the males used in the crosses belong to the strongest known Japanese races A and O (there is only a slight difference between these two which may be neglected here) and the females to the weak European races F and S, or the Japanese race H, all individuals genetically being females become transformed entirely into males. It may be added here that all results are based on fair numbers. For instance for this cross there are about 14 cultures with over 1000 individuals. In many cultures mortality is exactly recorded.

5. The following is to be regarded as an *experimentum crucis* for the correctness of the explanation given above: The Japanese race K proved to have a low potency of the male sex-factors, as crosses with European females produced normal offspring. Furthermore the same race K proved to be somewhat higher in potency than the European races by producing only the slightest degree of intersexuality in crosses with other males of the medium strong race G, whereas the European races gave in the corresponding cross with G-males up to high-grade intersexes. These same Europeans produce in the crosses with the strong races A and O nothing but males. Here we have an equation from which we should expect that in a cross between females from the races K and males A or O medium to high-grade intersexes will be produced. This is the actual result.

6. To these results may be added the following details:

a. The results are typical and, so far, without exception. They seem to be independent of external conditions as the same results were obtained identically (besides my former experiments carried on in Munich) in my cultures at the Bussey Institution, in Boston⁶ and those of my assistant Mr. Seiler in Berlin.

b. The grade of intersexuality in one culture is subject to a regular and continuous variation around a mean. If we divide the distance between femaleness and maleness in 100 grades a given culture would show a symmetric variation of a certain range, say 20 grades, around a mean of 50 or 60, etc. What causes certain differences in the position of the modal class in sister cultures is not yet clear, but will be very important for the theoretical side of the question. It is to be expected that at the two end points of the series the individuals overlap on the normal, *i.e.*, respectively normal females and males. This was actually found in the border cases. If all individuals which are genetically females are changed into males some minus individuals may be recognizable by their somewhat female shape of the wings, proving that the variability extends into the normal, too. It is to be hoped that the statistical treatment of these facts, together with the F_2 results and the data regarding the male intersexes will open a way to an exact calculation of the relative values of potency.

c. In the crosses producing nothing but males, occasionally there appears a single normal female, hatching as the last individual of a given culture. It is very probable that we face here another case of non-disjunction (Bridges). A spermatozoon without X-chromosome ought to give a normal female with every egg (assuming naturally that the male factors are carried in the X-chromosomes). So far I have succeeded only in finding a single spermatocyte II with 30 instead of 31 chromosomes.

So far only the facts regarding the female intersexes have been recorded, and they form a strong support for the views of my earlier papers in regard to the sex-problem. But the new results about the male intersexes show that in one important point the hypotheses have to be changed. I stated there that the male intersexes appear in F_2 from the reciprocal cross, not giving female intersexes in F_1 . The fact that exactly one-eighth of the males were intersexual corroborated strongly the Mendelian formula of sex-inheritance used by me, working with two pairs of sex factors. The new results give a different aspect to the facts:

1. The appearance of the male intersexes in the said crosses is a single event conditioned by the two races involved in the cross. The ratio $\frac{1}{8}$ is typical, too, only for the special combination. In other crosses any ratio between 0 and 50 percent may be typical.

2. A new fact of decisive importance is that male intersexes may be produced in F_1 . So there were a few individuals in the crosses female K \times male S and female O \times male H. And in the cross: weak Japanese female K \times weak Japanese male H, nothing but intersexual males appear in F_1 .⁶ These facts are of greatest importance for the whole question. Together with some other F_2 results and the insight in some former errors of interpretation they make it very probable that the female part of the formulae $F F M m = \varphi$

F F M M = ♂ does not mendelize but is inherited plasmatically. This part too shows different potencies and the final result is the combined effect of both groups. However, it seems undesirable to insist on this point, as the decisive experiments, which may bring the complete solution, have not yet been accomplished.

¹ Goldschmidt, R., Erblichkeitsstudien an Schmetterlingen. I., *Zs. induct. Abstammungslehre.*, 7, (1912); and Goldschmidt, R., und Poppelbaum, H., idem. II. *Ibid.*, 11 (1914)

² The existence of such local forms could be shown by breeding experiments. The problem of the geographical races of this moth has been for many years the object of my principal studies. However, the results are not yet ripe for publication.

³ Boveri, Th., Ueber die Entstehung der Eugsterschen Zwitterbienen., *Arch. Entw-Meck.*, Leipzig, 41 (1915).

⁴ The fact that male and female intersexes are different calls certainly for an explanation, but will not be discussed here. It may only be said that it is a question of the physiology of development.

⁵ I wish to express my sincerest thanks to Professor Wheeler and all the members of the staff of the Bussey Institution, Harvard University, for their kindness in granting me the facilities for prosecuting my work.

⁶ A similar cross with the same race H but another mother has been carried out already with the same result by Toyama's assistant, Dr. Machida, to whom therefore belongs the priority of this discovery. I am indebted to him, too, for the material of the race H. I do not know whether he has meanwhile published this result.

ON THE DEGREE OF INBREEDING WHICH EXISTS IN AMERICAN JERSEY CATTLE

By Raymond Pearl and S. W. Patterson

BIOLOGICAL LABORATORY, MAINE AGRICULTURAL EXPERIMENT STATION

Received by the Academy, December 17, 1915

In a series of 'Studies on Inbreeding' published during the past few years Pearl¹ has described in detail a method whereby it is possible to measure exactly the degree of inbreeding which exists in the pedigree of any particular individual animal. This is done by means of coefficients of inbreeding. These quantities may be defined as follows:

In the genetic passage from the $n + 1$ 'th ancestral generation to the n 'th, or in other words the contribution of the matings of the $n + 1$ 'th generation to the total amount of inbreeding involved in the production of an individual, the degree of inbreeding involved will be measured by the expression

$$Z_n = \frac{100 (p_{n+1} - q_{n+1})}{p_{n+1}} \quad (1)$$

where p_{n+1} denotes the maximum possible number of different individuals involved in the matings of the $n + 1$ generation, and q_{n+1} the *actual* number of different individuals involved in these matings. Z_n may be called a *coefficient of inbreeding*. If the value of Z for successive generations